THE ROLE OF PREDATION IN THE EVOLUTION OF CEMENTATION IN BIVALVES

by ELIZABETH M. HARPER

ABSTRACT. The independent appearance of many taxa of cementing bivalves during the early Mesozoic coincided with the marked increase in predation pressure described by Vermeij (1977, 1987). A causal link is implied by experimental work in which predators were offered the choice of byssate or cemented bivalve prey: cementation confers a significant selective advantage by inhibiting manipulability. The example illustrates the potential value to palaeontology of studies in behavioural ecology.

EPIFAUNAL bivalves attach to the substratum by two means: cementation by one valve or, more commonly, anchorage by byssal threads produced by the foot. Yonge (1962) believed that most, if not all, living bivalves possess a byssus in the larval stage, and that this structure was retained in some adults, for example the Mytilacea and the Arcacea, by neoteny. It would seem that the cemented habit in bivalves was evolved in stocks already possessing a functional adult byssus; indeed most living cementing bivalves, e.g. the Spondylidae and *Hinnites*, pass through a byssate stage in early ontogeny.

EXPERIMENTAL WORK

A series of experiments was designed to establish the relative vulnerability to predation of byssate and cemented bivalve prey. Asteroid and crustacean predators were offered the choice of bivalves attached both byssally and by cementation. *Mytilus edulis* was used for both prey types, so that any preference expressed would be due to mode of attachment only, rather than on the basis of different nutritional quality. Mussels with established byssal threads were collected intertidally in Dunstaffnage Bay, Oban, and cementation was simulated using an epoxy resin (Araldite Rapid – Ciba Geigy) to fix the shell by one valve to large blocks of substratum. These 'cemented' *Mytilus* fed normally and even produced superfluous byssus threads and hence behaved identically to the byssate individuals. Many byssate individuals were daubed with epoxy in order to monitor any inhibitory effect on predator behaviour (e.g. masking metabolite cues from the prey): no such effect was apparent. Treated and untreated specimens were eaten in equal proportions.

The experiments were run in outdoor running seawater tanks (1.5×0.8 m), each set up with a random distribution of the byssate and 'cemented' prey. A number of individuals of *Asterias rubens*, *Cancer pagurus* or *Carcinus maenas* were introduced into each tank, having previously been starved for at least four days. Regular observations were made on the feeding behaviour of the predators and any prey item taken was replaced with an identically attached individual. Hence the relative numbers of prey types were held constant.

RESULTS

If cemented and byssate prey were indistinguishable to predators, one might expect that they would be eaten in the proportions in which they occur in the tank (the null hypothesis). The results were in fact very different: a much higher proportion of prey taken was byssate (see Text-fig. 1). Chi-squared one-sample analysis of these results reveals that the preference for byssate prey over cemented was highly significant, rejecting the null hypothesis for *Asterias* and *Cancer* ($P \ll 0.001$),

PREDATOR	TOTAL NO. PREY TAKEN	NO. EXPECTED OF EACH	NO. BYSSATE EATEN	NO. CEMENTED EATEN	NO. PULLED FREE	P
Asterias rubens	121	60.5	95	11	15	<<0.001
Cancer pagurus	132	66	96	7	29	<<0.001
Carcinus maenas	27	13.5	19	4	4	<0.05

TEXT-FIG. 1. Experimental results of choice trials. Statistical analyses by χ^2. (All 'cemented' prey that was pulled free was treated in analysis as 'cemented'.) The null hypothesis that byssate and cemented prey are equally vulnerable to predation is rejected for *Asterias* and *Cancer* ($P \ll 0.001$), and for *Carcinus* ($P < 0.05$). The use of the binomial test confirms this significance.

and for *Carcinus* ($P < 0.05$). Binomial analysis was also employed in order to verify the significance and produced similarly significant levels. A number of the 'cemented' bivalves were pulled free and eaten. Statistically these were treated by including them with eaten 'cemented' prey, as Feifarek (1987) has demonstrated that during predation in the natural environment the right valve of *Spondylus americanus* may be broken from the substratum.

Observations showed that prey types were encountered according to their relative numbers in the tank. Rejection of 'cemented' prey was rapid, the predator moving on to tackle another individual. Some of the predators employed unorthodox methods of entry into the 'cemented' mussels. Instead of chipping in the manner described by Elner and Hughes (1978), *Carcinus* snipped along the ligament between the two valves without damaging them; *Asterias* broke valves in three instances. Hancock (1965) has also reported *Asterias* damaging mussels that were difficult to open.

DISCUSSION

Both predator groups used in this experiment need to manipulate their prey to feed. Chelate crustaceans use the chelae to assess the size of their prey and to locate weak points for attack. The rock lobster *Jasus edwardsii*, feeding on detached *Ostrea lutraria*, first holds the prey vertically and then reverses it (Hickman 1972). In the tanks both *Cancer* and *Carcinus* were observed to grasp the prey items in the master chela, rotating them around before pressure was applied to crush the valves. *Asterias* encountering *Mytilus* moves the prey so that the ventral valve margins of the shell are opposite its own oral region. Asteroids feed on bivalves by pulling the two valves apart with their arms and inserting stomach lobes in between the valves into the prey, thus feeding extraorally. In assuming the classic humped feeding position, the asteroid pulls the bivalve into a vertical position.

These results may be interpreted in terms of optimal foraging, as described by Krebs and Davies (1981), whereby predators are shown to choose prey that maximize the energy yield against energy expended to locate and subjugate it. The 'cemented' bivalves are less easy to manipulate than are those attached by a flexible byssus. Hence the effort required, and thus energy expended by the predator, is higher when dealing with cemented prey. Where byssate and cemented prey have the

same energy yield, it is preferable in terms of net energy gain for the predator to take the former. The unorthodox feeding methods employed by some of the *Asterias* and *Carcinus* may reflect a 'learned' response to deal with suboptimal prey. Cunningham (1983) reported that *Carcinus maenas* has a very rapid learning ability of altered feeding tactics.

Anecdotal evidence from the literature further demonstrates the advantages conferred by cementation on predation resistance. *Octopus dolfleini* prefers not to eat the cemented rock scallop, *Hinnites giganteus*, despite its presence close to the den (Hartwick *et al.* 1981), whilst crustaceans feeding on oyster spat are able to take a larger size of detached than of attached spat (Mackenzie 1970; Elner and Lavoie 1983). Feifarek (1987) detached *Spondylus americanus* and transplanted them into shallow water where they suffered a much higher mortality than on the reef. He attributed this to a higher vulnerability in shallow water, but it may equally well be interpreted as due to the decreased predator resistance of loss of attachment. Seastars cause extensive damage to oyster shellfisheries (Galtsoff and Loosanoff 1939), but commercially spat are detached at a very early stage in order to facilitate their harvest.

Although it is clearly possible for predators to eat cemented bivalves, the difficulty of manipulation compared with byssally attached bivalves, with their more flexible attachment, makes them less energetically favourable prey. It would seem intuitively obvious that a bivalve which becomes adapted for cementation will be selected for over evolutionary time.

IMPLICATIONS IN THE FOSSIL RECORD

More than sixteen families of bivalved mollusc have or have had representatives with the ability to cement to a hard substratum. Adaptations for cementation appear to have been acquired independently in over twenty clades. Some groups, for example the oysters and the extinct Mesozoic rudists, have been extremely successful over geological time.

It is traditional to view the habit as an adaptation to life in a turbulent environment (Kauffman 1969; Yonge 1979). Many byssate bivalve groups, however, also flourish in high energy conditions, for example the Mytilacea and the Arcacea. Udhayakumar and Karande (1986) have surveyed the relative strength of adhesion of various biofouling organisms: they showed that the force required to break the byssus threads of *Mytilus edulis* is considerably more per unit area than to sunder *Crassostrea cuculata*. Byssate attachment has a number of other advantages: the possibility of seasonally variable attachment strength (Price 1980); voluntary detachment for mobility, including secondary larval settlement; and the ability to reattach if dislodged accidentally. Cementation denies such advantages. In fact Nicol (1978) can determine 'no compelling reason to become shell cemented'.

Apart from the Pseudomonotidae, some of which cemented in the Carboniferous (Newell and Boyd 1972), cementation in bivalves is a post-Palaeozoic habit. Text-figure 2 shows the temporal distribution of the first independent appearance of the cementing bivalve groups. It appears that the Late Triassic and Jurassic were key times in the evolution of the habit. This pattern is strikingly coincidental with the first appearance of many durivorous predator groups during the Mesozoic and their diversification thereafter – the Mesozoic Marine Revolution (MMR) described by Vermeij (1977, 1987). Palmer (1982) has postulated that the increase in shelly epifauna in hardground communities during the Mesozoic may be due to predation rather than to scour resistance. Many notable molluscivores appeared during that time (see also Text-fig. 2). Although asteroid echinoderms evolved in the early Palaeozoic, it is suggested that it was not until the Triassic/Jurassic that the asteroids attained the suckered tube feet and the eversible stomach necessary for extraoral feeding (Blake 1981; Gale 1987). This ability to feed by prising the valves apart and extruding the stomach into the prey has made the modern seastars most voracious molluscivores. Palaeozoic seastars undoubtedly fed upon bivalved molluscs (Clark 1912), but probably only as scavengers.

Gastropods, in particular the drilling muricids and naticids, are also notable molluscivores. Drilling in these gastropod groups becomes prevalent from the Albian and Aptian stages of the Cretaceous (Taylor, Cleevely and Morris 1983; Taylor, Morris and Taylor 1986), although Fürsich

APPEARANCE OF THE
MOLLUSCIVOROUS HABIT   EVOLUTION OF CEMENTATION
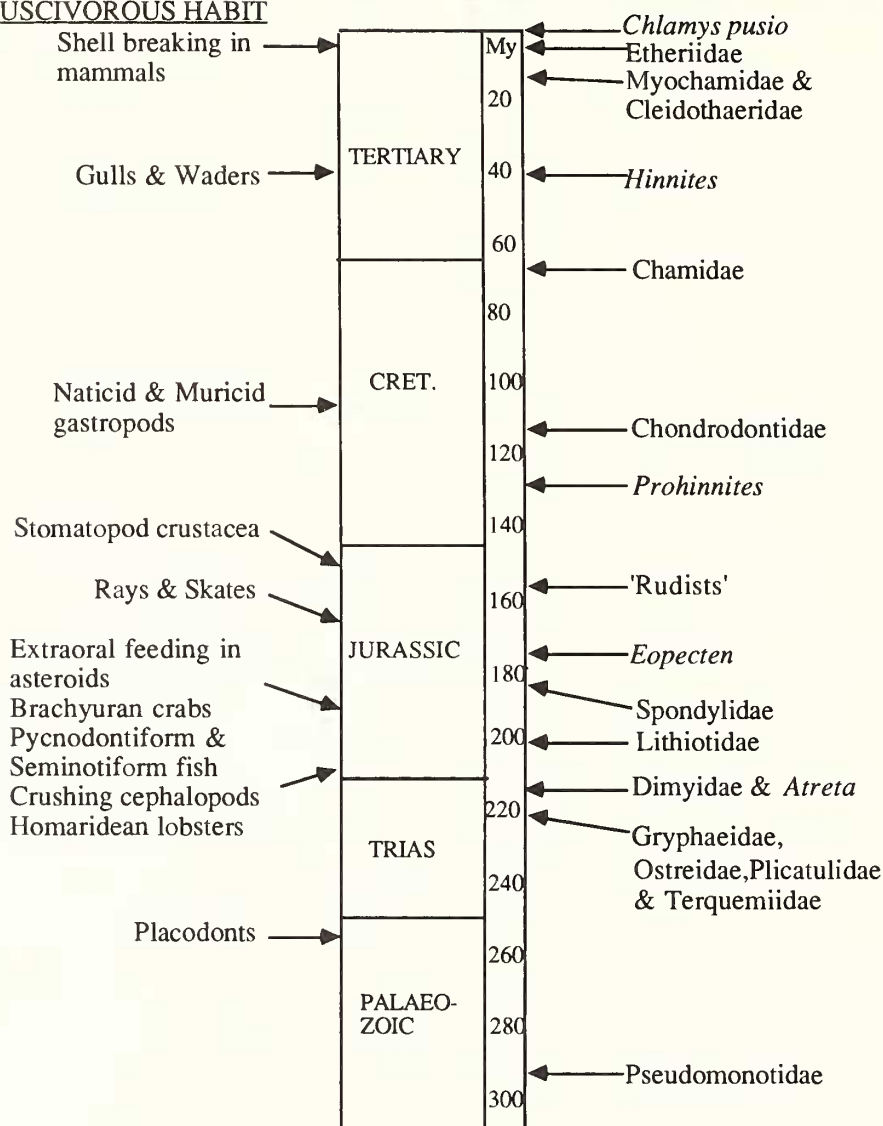
TEXT-FIG. 2. On the right is the temporal distribution of the first appearance of the cemented habit in independent clades in which the habit has been acquired, based on Skelton *et al.* (in press), figure 5 (data derived from personal records, Newell (1969), Waller (1978), Stenzel (1971), Skelton (1978), Newell and Boyd (1972) and Kennedy *et al.* (1970)). The timing of the appearance of various molluscivorous groups over geological time is plotted to the left, modified from Vermeij (1987).

and Jablonski (1984) report possible gastropod drill holes from the Triassic. It seems likely that this mode of predation which involves little manipulation would not be hampered by cementation. Their appearance in the Cretaceous is not marked by further proliferation of cemented taxa. However, further experiments are envisaged using gastropod predators.

The experimental evidence described here gives a strong suggestion that the appearance of many

cemented bivalve taxa at the same time as the start of the MMR may not be coincidental. If not a primary selective force favouring the initiation of cementation, then the increased predator resistance must at least have been a valuable evolutionary spin-off.

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